

## Young frigatebirds learn how to compensate for wind drift

Joe Wynn, Julien Collet, Aurélien Prudor, Alexandre Corbeau, Oliver Padget, Tim Guilford and Henri Weimerskirch

### Article citation details

*Proc. R. Soc. B* **287**: 20201970.  
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### Review timeline

Original submission: 12 August 2020  
Revised submission: 28 September 2020  
Final acceptance: 28 September 2020

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

## Review History

### RSPB-2020-1970.R0 (Original submission)

#### Review form: Reviewer 1

##### Recommendation

Accept with minor revision (please list in comments)

##### Scientific importance: Is the manuscript an original and important contribution to its field?

Excellent

##### General interest: Is the paper of sufficient general interest?

Excellent

##### Quality of the paper: Is the overall quality of the paper suitable?

Excellent

##### Is the length of the paper justified?

Yes

##### Should the paper be seen by a specialist statistical reviewer?

No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**

No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**

Yes

**Is it clear?**

Yes

**Is it adequate?**

Yes

**Do you have any ethical concerns with this paper?**

No

### **Comments to the Author**

I have to congratulate the authors for their work. This ms shows amazing findings that can be interesting for a very wide readership. The study design is very sophisticated, the sample size is quite high, and the conclusions agree with the results. I don't have major concerns, but just some minor comments.

I don't know well the natural history of the studied species, and I wonder if they forage lonely or in groups and, in the latter case, how the authors can discard any importance of social learning by juveniles to correct for drift. I know, the results speak very clearly that experience and landmarks are determinant, but a sentence to exclude interactions with adults should be reported.

Methods: the brand and model of the GPS devices must be reported.

Line 81: why the rolling median and not the exact altitude of the fix? May be because fixes were not real but interpolated?

Line 133: is there a missing word? After "per", do you miss "individual"?

Line 212-214. May be I don't understand well, but probably there is a typo: I guess you want to say, in this case, that you don't find explanation to the fact that drift increases with visible landmarks. By the way, I agree with the following explanation about birds "relaxing" when approaching the colony.

## **Review form: Reviewer 2 (Jason Chapman)**

### **Recommendation**

Accept with minor revision (please list in comments)

**Scientific importance: Is the manuscript an original and important contribution to its field?**

Good

**General interest: Is the paper of sufficient general interest?**

Good

**Quality of the paper: Is the overall quality of the paper suitable?**

Excellent

**Is the length of the paper justified?**

Yes

**Should the paper be seen by a specialist statistical reviewer?**

No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**

No

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Yes

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Yes

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This is a very interesting paper which provides a rare example of improvement in navigation capability (specifically, ability to compensate for cross-winds during homing) in birds. I really liked this paper, it was well written and provides a clear and strong demonstration of the key results. I only have minor comments which the authors could consider when producing the next draft.

1. on line 45, I think 'goal' might be better than 'home', as many species employ wind compensation on journeys where they are heading to a goal or general area which is not necessarily their permanent home.
2. Methods (lines 98-100) & Results (line 133). I was a bit confused about the number of trips contained in the analyses. The methods state: "In total, 19,732 interpolated GPS fixes were used in the analysis of fledgling frigatebirds, representing 363 trips from 10 individual birds, whilst 35,430 interpolated GPS fixes were used in the analysis of adult frigatebirds, representing 135 trips from 13 individuals". To my understanding, this comes out at a mean of 36 trips per individual juvenile bird, and 10 per individual adult. In the results, however, it is stated that the median number of trips per juvenile bird was 127 (plus/minus 16), and I couldn't see the respective figure for adults. Have I misinterpreted something here, or is something awry with the description in the methods? This needs to be clarified. In addition, the statement on line 133 appears to be missing a word after 'per'? (i.e. text reads, "trips per over the fledgling period").
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Figs 2 & 3 - it would be better to label the panels as to whether they are adult/juvenile and in sight / not in sight of land, for clarity. Also, the use of different scales on Fig 3 seems to indicate that the slope is steeper when land is visible, when in reality I suspect the opposite is true.

## Decision letter (RSPB-2020-1970.R0)

11-Sep-2020

Dear Mr Wynn:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into <http://mc.manuscriptcentral.com/prsb> and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" - in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

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If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

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Best wishes,  
Professor Gary Carvalho  
<mailto:proceedingsb@royalsociety.org>

Associate Editor

Comments to Author:

Both reviewers really enjoyed reading your manuscript and felt that you have made significant and interesting advances, and I agree! They have only a few minor suggestions for improvements, and these should be addressed prior to publication.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

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Referee: 2

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Figs 2 & 3 - it would be better to label the panels as to whether they are adult/juvenile and in sight / not in sight of land, for clarity. Also, the use of different scales on Fig 3 seems to indicate that the slope is steeper when land is visible, when in reality I suspect the opposite is true.

## Author's Response to Decision Letter for (RSPB-2020-1970.R0)

See Appendix A.

## Decision letter (RSPB-2020-1970.R1)

28-Sep-2020

Dear Mr Wynn

I am pleased to inform you that your manuscript entitled "Young frigatebirds learn how to compensate for wind-drift" has been accepted for publication in *Proceedings B*.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

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Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,  
Professor Gary Carvalho  
Editor, Proceedings B  
mailto: [proceedingsb@royalsociety.org](mailto:proceedingsb@royalsociety.org)

Associate Editor:  
Board Member  
Comments to Author:  
(There are no comments.)

## **Appendix A**

*Dear editor-in-chief,*

*Many thanks for the return of our manuscript with reviewer input, and many thanks to the anonymous reviewers for their comments (which we have now incorporated). Please find below a point-by-point response to each reviewer's comments. Reviewer comments are in italics, our responses in plain text and exerts from our amended manuscript in bold.*

*We hope you enjoy reading our revised manuscript.*

*Many thanks and best wishes,*

*Joe*

**Reviewer(s)' Comments to Author:**

**Referee: 1**

*Comments to the Author(s)*

*I have to congratulate the authors for their work. This ms shows amazing findings that can be interesting for a very wide readership. The study design is very sophisticated, the sample size is quite high, and the conclusions agree with the results. I don't have major concerns, but just some minor comments.*

We thank reviewer #1 for their positive comments regarding the manuscript.

*I don't know well the natural history of the studied species, and I wonder if they forage lonely or in groups and, in the latter case, how the authors can discard any importance of social learning by juveniles to correct for drift. I know, the results speak very clearly that experience and landmarks are determinant, but a sentence to exclude interactions with adults should be reported.*

As a colonially nesting seabird it is possible that social learning could be involved in how individuals learn to compensate for wind drift, with inexperienced birds using the behaviour of experienced individuals to reduce their own wind drift. We have amended our manuscript to reflect this possibility (lines 185-188):

**“Although these effects are consistent with processes dominated by individual learning it is also possible that social learning effects, learning involving the observation and mimicry of conspecifics (37), might also contribute since frigatebirds are a colonially-nesting species.”**

*Methods: the brand and model of the GPS devices must be reported.*

Amended (line 78 in the amended manuscript).

*Line 81: why the rolling median and not the exact altitude of the fix? May be because fixes were not real but interpolated?*

A rolling median was used because altitude was derived from GPS data, meaning that there was likely significant error in each estimate of altitude. As such, given that the altitude observed at a given position along a trajectory is necessarily influenced by the altitude observed in the prior and subsequent points, we reasoned that a rolling median would reduce error in the estimate of altitude for each fit. We have summarised and included this point in our revised manuscript, and have added the citations upon which this rationale is based (lines 88-90).

*Line 133: is there a missing word? After “per”, do you miss “individual”?*

This was indeed a typo and has been amended (line 104; when responding to reviewer #2's comment we have repositioned this sentence).

*Line 212-214. May be I don't understand well, but probably there is a typo: I guess you want to say, in this case, that you don't find explanation to the fact that drift increases with visible landmarks. By the way, I agree with the following explanation about birds “relaxing” when approaching the colony.*

As the reviewer suggests, we find the result that adult frigatebirds drift more with the wind when in sight of the colony puzzling and, consequently, suggest that this might not be because their navigational ability is compromised by visual cues but might, instead, reflect changes in motivation. We have rewritten this paragraph in order to make this hypothesis clearer (lines 219-224):

**“However, the magnitude of this difference is substantially smaller (by almost an order of magnitude) than the difference observed in fledglings. Given that there is no apparent sensory explanation why drift might be reduced with increased salient visual information in experienced individuals, we suggest that such a difference may reflect differences in the motivation to home when approaching the colony rather than an inability to compensate for drift when in-sight of land.”**

***Referee: 2***

*Comments to the Author(s)*

*This is a very interesting paper which provides a rare example of improvement in navigation capability (specifically, ability to compensate for cross-winds during homing) in birds. I really liked this paper, it was well written and provides a clear and strong demonstration of the key results. I only have minor comments which the authors could consider when producing the next draft.*

We thank reviewer #2 for their positive comments on the submitted manuscript.

*1. on line 45, I think 'goal' might be better than 'home', as many species employ wind compensation on journeys where they are heading to a goal or general area which is not necessarily their permanent home.*

We agree with that all goalwards movement is not ‘homing’ and have amended the sentence to appropriately reflect this (line 47).

*2. Methods (lines 98-100) & Results (line 133). I was a bit confused about the number of trips contained in the analyses. The methods state: "In total, 19,732 interpolated GPS fixes were used in the analysis of fledgling frigatebirds, representing 363 trips from 10 individual birds, whilst 35,430 interpolated GPS fixes were used in the analysis of adult frigatebirds, representing 135 trips from 13 individuals". To my understanding, this comes out at a mean of 36 trips per individual juvenile bird, and 10 per individual adult. In the results, however, it is stated that the median number of trips per juvenile bird was 127 (plus/minus 16), and I couldn't see the respective figure for adults. Have I misinterpreted something here, or is something awry with the description in the methods? This needs to be clarified.*

We thank the reviewer for point out this confusing and contradictory series of assertions, which is the result of an arithmetic error. Upon subsequent examination it is apparent that instead of there being 363 trips overall, there are in fact 1001 trips in total. We have amended the manuscript to reflect this, and have included both mean and median numbers of trips for adults and chicks (lines 104 to 107):

**“In total, 19,732 interpolated GPS fixes were used in the analysis of fledgling frigatebirds, representing 1001 trips from 10 individual birds (with a mean of 100 and a median of 122 trips per individual), whilst 35,430 interpolated GPS fixes were used in the analysis of adult frigatebirds, representing 345 trips from 13 individuals (with a mean of 26 and a median of 12 trips per individual).”**

*In addition, the statement on line 133 appears to be missing a word after 'per'? (i.e. text reads, "trips per over the fledgling period").*

Amended (line 104).

*3. line 205, should 'per-migratory' read 'pre-migratory'?*

We thank the reviewer for pointing out this error, this has now been corrected (line 214).

*4. the use of references was fine, but rather bird-focussed, and I wondered if a few lines and well-chosen references might not make the paper of wider relevance, if comparisons were drawn with capabilities & similarities with other taxa. In particular, i am thinking about (i) the striking similarity in the effect of trip number on orientation capabilities that have been seen in inexperienced honeybee workers (e.g. Capaldi et al 2000, Ontogeny of orientation flight in the honeybee revealed by harmonic radar, Nature); and (ii) the role of landmarks (coastlines) in correcting for current drift in homing sea turtles (several papers from e.g. Graeme Hays & colleagues, plus other groups).*

We agree that the inclusion of non-avian examples of drift compensation/navigational ontogeny in the introduction would broaden the appeal of this manuscript. Consequently, we have chosen to include the suggested references pertaining to turtles and bees, alongside several relating to both large-scale and small-scale drift compensation in teleost fish, Hymenoptera and migratory Lepidoptera (references 10, 11, 12, 13, 14 and 23). Further, we have generalised the noun usage in the abstract and introduction to reflect the broader relevance of our findings.

*Figs 2 & 3 - it would be better to label the panels as to whether they are adult/juvenile and in sight / not in sight of land, for clarity. Also, the use of different scales on Fig 3 seems to indicate that the slope is steeper when land is visible, when in reality I suspect the opposite is true.*

We agree with the reviewer's observation that labelled panels would reduce confusion and have, consequently, amended the plots and legends accordingly. Regarding the scaling of the 2 panels in figure 3 the reviewer is correct in their assertion that the scaling on the y-axes makes the right-hand plot look steeper than it is. Consequently, we have amended the y-axes and moved the line labels to an external legend insert (figures 2 and 3).